

Effect of overnight temperature on leaf photosynthesis in seedlings of *Swietenia macrophylla* King

ZHANG Cheng-Jun¹, Carlos Henrique B. de A. Prado², ZU Yuan-Gang¹, GUO Jia-Qiu³, Carlos Cesar Ronquim², Leonnardo Lopes Ferreira²

¹ Key Laboratory of Forest Plant Ecology, Northeast Forestry University, Harbin 150040, P. R. China

² Laboratory of Plant Physiology, Department of Botany, Federal University of Sao Carlos, SP, 13565-905, Brazil

³ The Second Affiliated Hospital of Harbin Medical University, Harbin 150086, P. R. China

Abstract: After exposure of one-year old seedlings of *Swietenia macrophylla* to an overnight temperature (13 °C, 19 °C, 25 °C, 31 °C or 35 °C), the leaf net photosynthetic rate (P_n) was researched through measuring photosynthetic light-response curves at 360 $\mu\text{mol} \cdot \text{mol}^{-1} \text{CO}_2$, and photosynthetic CO_2 -response curves at light-saturated intensity (1500 $\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$). The optimal temperature for photosynthesis measured at 360 $\mu\text{mol} \cdot \text{mol}^{-1} \text{CO}_2$ was from 25 °C to 31 °C, but which was from 31 °C to 35 °C at saturating CO_2 concentration. At temperature of below 25 °C, the decline in P_n was mainly due to the drop in carboxylation efficiency (C_e), while as temperature was over 31 °C, the reduction in P_n resulted from both decrease in C_e and increase in leaf respiration. The CO_2 -induced stimulation of photosynthesis was strongly inhibited at temperatures below 13 °C. The results showed that, the leaf photosynthesis of tropical evergreen plants should not be accelerated at low temperature in winter season with elevated CO_2 concentration in the future.

Keywords: Apparent quantum yield; Carboxylation efficiency; CO_2 -induced stimulation; *Swietenia macrophylla* King; Leaf temperature

CLC number: Q945.11

Document code: A

Article ID: 1007-662X(2003)02-0130-05

Introduction

Leaf photosynthesis is one of the most thermal sensitive processes providing an indicator for functional limitations imposed particularly by air temperature (Harley 1995). At temperatures too high or too low the photosynthetic yields decrease steadily until CO_2 uptake ceases (Larcher 1994). Plants are exposed to only a narrow range of temperatures at most tropic regions, so even smaller changes in temperature might be equal or more important in the tropics than at temperate latitudes (Hogan *et al.* 1991). However, very little attention has been directed to the photosynthetic response of tropical trees to the interactions between temperature and irradiance, as well as between temperature and CO_2 concentrations (Hogan *et al.* 1991).

Big-leafed Mahogany (*Swietenia macrophylla* King (Maliaceae)) is distributed naturally from the south of Mexico throughout Central and South America to Bolivia and Brazil, including large portions of the Amazon Basin. It is one of the most valuable plants on the international market because of the beauty and durability of its wood. Increasing demand for this valuable timber has resulted in a severe decline in the wild population of this species (Schmidt *et al.* 2000). Thus, it is necessary to determine its ecophysiological properties, especially to predict its possible response in the future with increasing CO_2 and temperature.

This work was to determine the response of net photosynthetic rate in *Swietenia macrophylla* seedlings to leaf temperature, through measuring photosynthetic light-response curves and photosynthetic CO_2 -response curves at light-saturated intensity, following an overnight temperature (13 °C, 19 °C, 25 °C, 31 °C or 35 °C, which is similar to the annual air temperature scope in the natural habitat of this species). Considering CO_2 -temperature interaction we predicted that the optimal temperature of photosynthesis in this tropical species might also be shifted upward at high CO_2 concentration like most temperate plants.

Materials and methods

The one-year-old seedlings of *Swietenia macrophylla* were cultivated in polystyrene foam boxes containing 32 kg sifted cerrado soil. Five boxes of seedlings were used for experiment, two seedlings per box. They were grown in a greenhouse with diurnal temperature (25 ± 5) °C, night temperature (18 ± 3) °C and relative humidity (RH, $(60 \pm 10)\%$). During the experimental period the seedlings cultivated in the soil was irrigated well once a week.

Preliminary experiment showed that photosynthesis measured at similar conditions was similar for leaves with similar age in these seedlings. Before temperature treatment, two boxes were wrapped with a thick synthetic mantle in order to maintain the soil temperature constant. Thus, only the aerial parts of plants were exposed to the desired temperature. The two boxes were placed into an incubator (Model NT-708, Piracicaba, Brazil) at a temperature set as

Biography: ZHANG Cheng-Jun (1968-), male, Lecturer in Key Laboratory of Forest Plant Ecology, Northeast Forestry University, Harbin 150040, P. R. China.

Received date: 2003-03-11

Responsible editor: Zhu Hong

13 °C, 19 °C, 25 °C, 31 °C or 35 °C. The treatment started from 19:00 to 7:00. The interval between two treatments was at least one week for each box.

Leaf photosynthesis was conducted in a special chamber with similar temperature as the treating level in the following morning from 7:00 to 9:00. The healthy mature leaves with similar age were chosen to measure photosynthetic light-response curves using a portable infra-red gas analyzer (LCA-4 model, ADC, Hoddesdon, UK) with a Parkinson Leaf Chamber (PLC4-N). The light started from 2000 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ to 0 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, provided by a Portable Light Unit (PLU-002, ADC) mounted on the head of the PLC4-N. The leaf temperature was maintained by a microclimate controller (PLC4-TC, Peltier cooler/heater system, ADC) at the night treating temperature. Six to seven stable values were recorded at one light level. To prevent stomatal closure, relative humidity in the leaf chamber was maintained at 45 % obtained from the preliminary experiment.

Measurements of leaf gas exchange as a function of CO_2 concentrations (P_n/C_a and P_n/C_i curves) were carried out by an ADC gas diluter (GD-602-GC), which can produce a series of intermediate CO_2 concentrations from a single cylinder containing 1900 $\mu\text{mol}\cdot\text{mol}^{-1}$ CO_2 . Eleven levels of CO_2 concentration were available, varying from 1900 $\mu\text{mol}\cdot\text{mol}^{-1}$ to 0 $\mu\text{mol}\cdot\text{mol}^{-1}$ and diluting at 10 % intervals. The light was maintained at a saturating value of 1500 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ during P_n/CO_2 curves according to photosynthetic light-response curves previously obtained. The measurement was still made in the special chamber and the control of leaf temperature was similar to the measurement of photosynthetic light-response curves.

The non-linear adjustment of photosynthetic light-response curves followed the model described by Prado *et al.* (1997).

$$P_n = P_1 \times (1 - e^{-P_2 \times (x - P_3)}) \quad (1)$$

where P_1 is the light-saturated photosynthetic rate ($P_{n\text{max}}$, $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$), P_2 is a constant, P_n is the actual photosynthetic rate ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$), x is the photosynthetic photon flux density ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$), P_3 is the light compensation point (L_{cp} , $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$), and e is the natural logarithm. The light saturation point (L_{sp} , $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) was calculated at 90 % of $P_{n\text{max}}$. Leaf respiration in the dark (R_d) was obtained at 0 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ photosynthetic photon flux density. The estimation of apparent quantum yield of CO_2 assimilation (Φ) was obtained from the following equation derived from the inclination of the straight line in the first linear phase of the curve obtained from equation (1), (Prado *et al.* 1997).

$$\Phi = P_1 \times P_2 \times e^{P_2 \times P_3} \quad (2)$$

Similarly, the two equations were also used to fit P_n/C_a and P_n/C_i responses and to obtain the corresponding parameters: light- and CO_2 -saturated photosynthetic rate ($P_{n\text{max}}$, $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$), CO_2 saturation point (C_{sp} ,

$\mu\text{mol}\cdot\text{mol}^{-1}$), CO_2 compensation point (C_{cp} , $\mu\text{mol}\cdot\text{mol}^{-1}$), carboxylation efficiency (C_e , $\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$), and leaf respiration in the light (R_l , $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$).

Results

At 360 $\mu\text{mol}\cdot\text{mol}^{-1}$ CO_2 , the response of P_n to photosynthetic photon flux density varied depending on leaf temperature (Fig. 1). The curve of $P_{n\text{max}}$ to leaf temperature showed a typical shape with an optimal maximum, and supra- and sub-optimal depression (Fig. 2). The optimal temperature for net photosynthetic rate was observed between 25 °C and 31 °C. As leaf temperature decreased from 25 °C to 13 °C, $P_{n\text{max}}$ decreased. Supra-optimal temperature above 31 °C inhibited leaf photosynthesis.

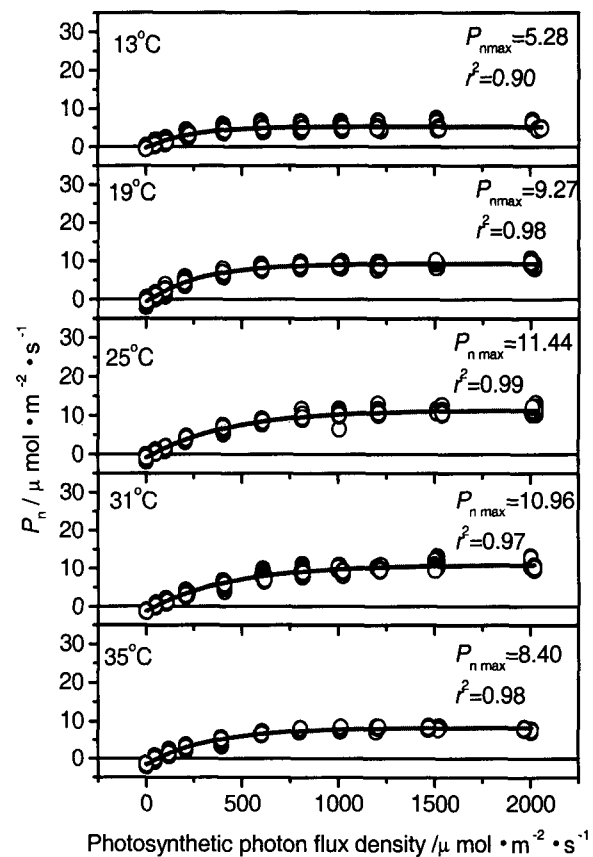


Fig. 1 Net photosynthesis (P_n) as a function of photosynthetic photon flux density in *Swietenia macrophylla* seedlings following overnight leaf temperature treatment. Each curve was obtained by fitting the data of two or three replicates for each temperature level.

The variation in L_{sp} response to temperature was positively related to that in $P_{n\text{max}}$ response ($r=0.88$, $p<0.05$) (Fig. 2B). The relatively high values of L_{sp} were observed at 25 °C and 31 °C at the higher values of $P_{n\text{max}}$, while the lowest value occurred at 13 °C with the lowest value of $P_{n\text{max}}$. R_d increased with increasing temperature (Fig. 2E), which resulted in a paralleling response of L_{cp} (Fig. 2C). Φ increased from 13 °C to 19 °C, but decreased from 19 °C to 25 °C and then maintained relatively constant from 25 °C to

35 °C (Fig. 3D).

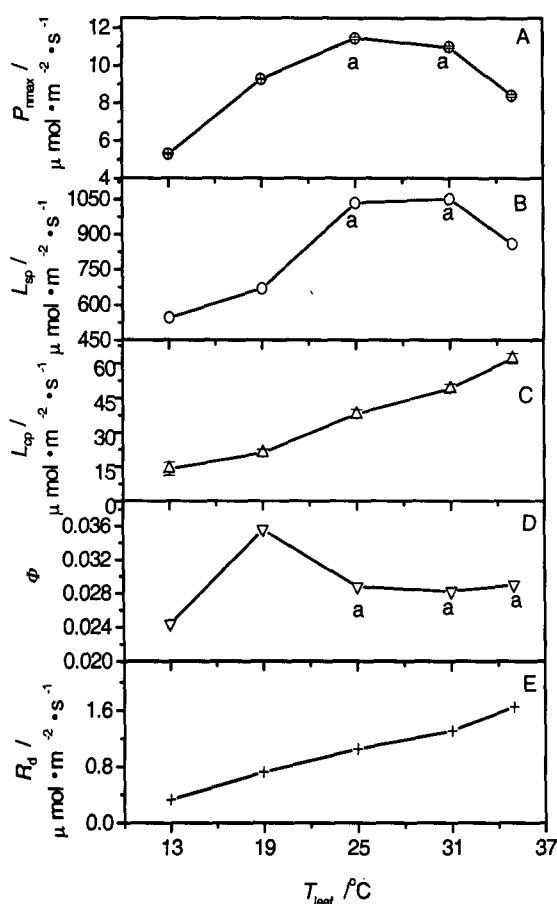


Fig. 2 The temperature response of light-saturated photosynthetic rate (P_{\max}), light saturation point (L_{sp}), light compensation point (L_{cp}), apparent quantum yield (Φ) and respiration in the dark (R_d) in *Swietenia macrophylla* seedlings. All parameters were obtained from photosynthetic light-response curves. Vertical bars indicate the standard deviation. The same small letters below symbols indicate that the difference in the values in every row figure are not significantly at the level of $P < 0.05$.

At different overnight temperatures, the photosynthetic responses, as a function of C_i at a saturating light of $1500 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, are shown in Fig. 3. At light- and CO_2 -saturated conditions, within the experimental temperature ranges, the leaf photosynthesis rate increased with increasing temperature from 13 °C to 31 °C, the optimal temperature was selected between 31 °C and 35 °C (Fig. 3 and 4A). The C_{sp} , as well as C_{cp} , decreased from 13 °C to 19 °C, and then increased from 19 °C to 35 °C (Fig. 4B-C). C_e increased from 13 °C to 31 °C, and was inhibited at 35 °C. R_i at a light of $1500 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ increased as temperature rose from 13 °C to 35 °C.

Discussion

In this work, different overnight leaf temperatures caused large variation in Φ in the following day. Ehleringer *et al.* (1993) pointed out that two environmental parameters most

likely to influence any change in Φ would be temperature and irradiance during seedling growth. In this work, therefore, variation in Φ was mainly attributable to different overnight leaf temperatures. Based on theoretical expectation, Φ should be decreased with increasing temperature from 15 °C to 40 °C (Long 1991), which has been confirmed by some studies (Cannell *et al.* 1998). However, the Φ increased between 13 °C and 19 °C, and was stable between 25 °C and 35 °C in the present work. The results are contrary to such a theoretical expectation (Fig. 2D). The conflict between theoretical expectation and experimental results for Φ was also observed in *Glycine max* by Harley *et al.* (Leegood *et al.* 1996). They found that Φ did not decrease until temperatures exceeded 25 °C. This kind of phenomenon may be explained by the differences in prevailing growth temperatures. The values of Φ decreased as leaf temperature decreased from 19 °C to 25 °C (Fig. 2D), which may be mainly attributable to photorespiration (Fig. 3E) resulting in reduction in assimilation power (Long 1991; Cannell *et al.* 1998).

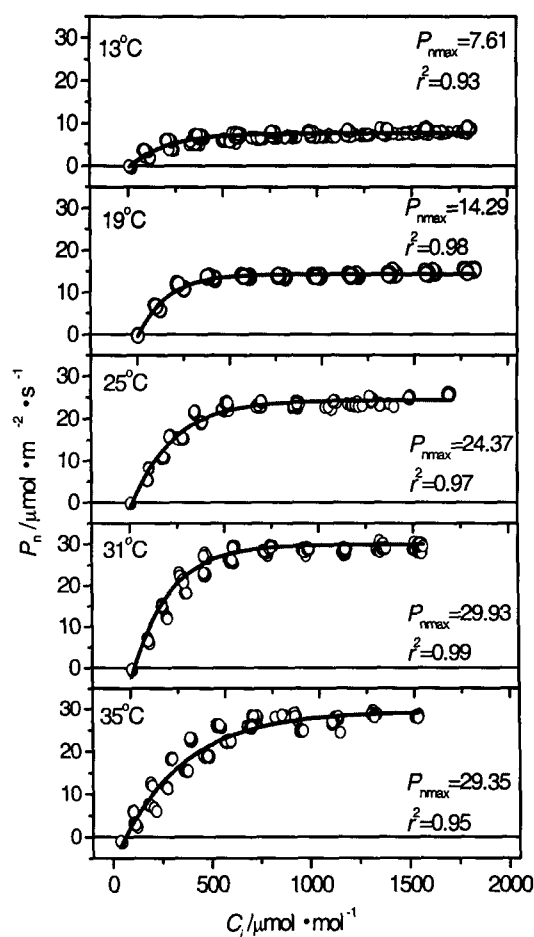


Fig. 3 Net Photosynthetic rate (P_n) as a function of leaf intercellular CO_2 concentration (C_i) in *Swietenia macrophylla* seedlings following overnight leaf temperature treatment. All curves were made at $1500 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ photosynthetic photon flux density, 45 % RH. Each curve was obtained by fitting the data of two or three replicates for each temperature level.

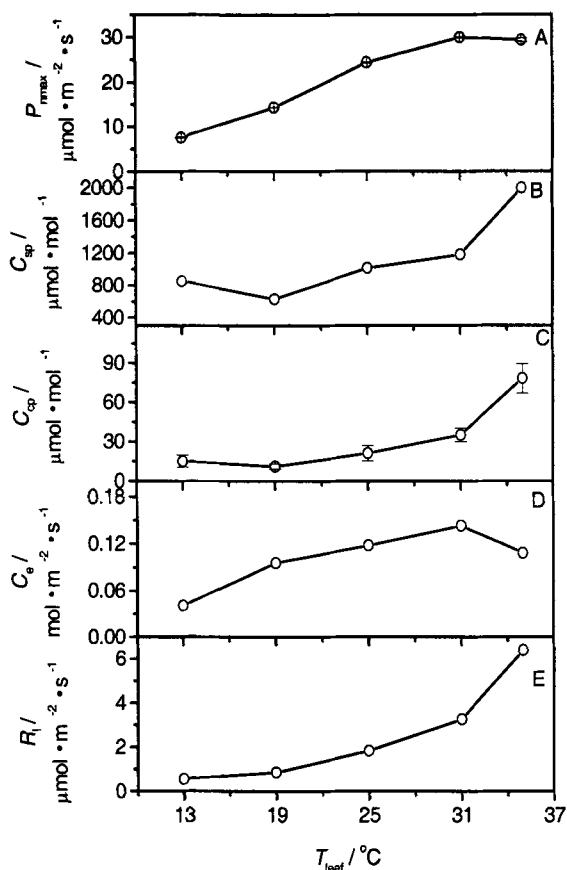


Fig. 4 The temperature response of photosynthetic rate (P_{nmax}) at light- and CO_2 -saturated points, CO_2 saturation point (C_{sp}), CO_2 compensation point (C_{cp}), carboxylation efficiency (C_e) and respiration in the light (R_l) in *Swietenia macrophylla* seedlings. The values of P_{nmax} , C_e and R_l were obtained from P_n/C_i curves, while C_{sp} and C_{cp} values from P_n/C_a curves (omitted). Vertical bars indicate the standard deviation.

The C_e increased as temperature rose from 13 °C to 31 °C (Fig. 4D), which may be attributable to increased capacity of the enzymes of carbon assimilation (Leegood *et al.* 1996). In general, increasing temperature increases not only the carboxylation capacity of Rubisco, which has a positive effect on C_e , but also the K_m (Michaelis-Menten constant) of Rubisco for CO_2 , which has a negative effect on C_e (Edwards 2002, personal communication). An additional negative effect on C_e may result from the increase in the competitive capacity of O_2 for Rubisco which could be reflected by increased leaf respiration (Fig. 2E) with increasing temperature. The increase in C_e between 13 and 31 °C showed that the positive effect of increasing temperature was greater than its negative effect on C_e in this study. The C_e at 35 °C was reduced most probably because higher leaf temperature decreased the CO_2 specificity of Rubisco and increased O_2 specificity of Rubisco in favor of oxygenase (Bowes 1991).

It has been well documented that the temperature optimum for photosynthesis is always associated with the temperature range prevailing in the native habitat of plants (Björkman *et al.* 1972; Chabot *et al.* 1976; Mooney *et al.* 1976). In this work, measured at ambient CO_2 , the optimal temperature for leaf net photosynthesis was between 25 °C

and 31 °C (Fig. 2A), which is within the range of optimal leaf photosynthetic temperature for most tropical plants (Larcher 1994).

Light-saturated photosynthetic rate is determined by carboxylation and RuBP-regeneration capacities (Mooney *et al.* 1976). Inhibition of carboxylation capacity was directly related to inhibition of photosynthesis and could have a significant effect on plant growth and development (Law *et al.* 1999). In this work, measured at ambient CO_2 and temperatures between 25 °C and 31 °C (Fig. 2A), the highest photosynthesis was simultaneously with the higher values both in C_e and L_{sp} (Fig. 2D and 3D). Therefore, the higher value of P_{nmax} can be entirely attributable to the highest carboxylation capacity of Rubisco because at low C_i and high light ($> 1000 \mu mol \cdot m^{-2} \cdot s^{-1}$) photosynthesis is likely to be limited almost exclusively by Rubisco (Higuchi *et al.* 1999).

It is well documented that declines in photosynthesis following a low temperature in dark or light have been attributed partly to decline in Rubisco activity (Allen *et al.* 2001), while high temperatures inhibit photosynthetic CO_2 fixation and damage photosynthetic electron transport, particularly at the site of PSII (He *et al.* 2001). Compared with the value of P_{nmax} at the optimal temperature, the photosynthesis decreased significantly with decreasing leaf temperature from 25 °C to 13 °C (Fig. 2A). The decrease in P_{nmax} at sub-optimal temperature mainly resulted from the substantial decline in C_e by lower leaf temperature (Fig. 4D). In contrast, inhibition of P_{nmax} at supra-optimal temperature was mainly due to both reduction in carboxylation capacity of Rubisco and the sharp increase in leaf photorespiration (Fig. 2A and 3D-E).

The results here also showed that high CO_2 concentration increased leaf photosynthesis and that its stimulatory magnitude was dependent on leaf temperature. At instantaneous high CO_2 concentration, the increase in photosynthesis in C_3 plants is usually attributed to increased intercellular CO_2 concentration which leads to increase both in C_e (Drake *et al.* 1997) and in Φ (Cannell *et al.* 1998), and decrease in photorespiration (Law *et al.* 1999).

At saturating light intensity, increasing leaf temperature from 13 °C to 31 °C resulted in an increase in photosynthetic capacity, C_e and leaf respiration. The higher values of P_{nmax} were observed between 31 °C and 35 °C (Fig. 3 and 4A), suggesting that high CO_2 resulted in an upward shift in the photosynthetic temperature optimum of this species studied. The result is consistent with our prediction. The CO_2 -induced upward shifts in optimal temperatures for photosynthesis were also reported with other C_3 plants (Sheu *et al.* 1999) and consistent with theoretical prediction (Mitchell *et al.* 2000). Although high temperatures alter the CO_2/O_2 specificity of Rubisco in favor of oxygenase, increasing the CO_2 concentration reduces the oxygenase activity of Rubisco, favoring increased net CO_2 fixation and as a consequence CO_2 enrichment increases the temperature optimum for photosynthesis (Bowes 1991). These

results also confirm the prediction of Long (1991) that the temperature optimum of P_{nmax} must increase with ambient CO_2 increment. The shift in optimal temperatures underlies that the importance of considering rise in atmospheric CO_2 , not simply as a factor which increases photosynthetic rate, but also as a variable that modifies the response to temperature (Long 1991), and which confirms that high CO_2 concentration can diminish high temperature inhibition of photosynthesis (Hogan *et al.* 1991).

It is also apparent that the magnitude of CO_2 -induced increase in photosynthesis at higher temperatures is greater than that at lower temperatures (Fig. 2), which is consistent with the concept that inhibition of oxygenation by rising CO_2 concentration and hence increase in net photosynthesis will have its greatest effect at higher leaf temperatures because CO_2 -induced changes in photorespiration and Rubisco activity are greater at high than at low temperatures (Greer *et al.* 2000). Similarly, this result also shows that at lower temperatures, the stimulation effect of high CO_2 can be reduced (Fig. 1 and Fig. 3), which further confirms that low temperatures will necessarily reduce the relative stimulation of photosynthesis caused by rising atmospheric CO_2 (Bunce 2000). And this also indicates that CO_2 -temperature interactions is smaller at lower temperatures (Cannell *et al.* 1998). Similar results were observed with loblolly (*Pinus taeda*), (Hymus *et al.* 1999). Hymus *et al.* (1999) pointed out that elevated CO_2 concentration might add a further stress to overwintering evergreen vegetation in temperate regions. Our result showed that such an effect may also occur in tropical regions.

According to the inhibition of CO_2 -induced stimulation of photosynthesis by low temperature and the upward shift in temperature optimum by increasing C_a , it is easy to conclude that the winter stress on evergreen foliage in tropics might be greater than in temperate regions because the sub-optimal temperature range for photosynthesis will be wider in tropical area than in temperate regions in terms of the degree of the increase in temperature in the future.

Acknowledgements

This study was carried out when Zhang Chengjun as a visiting scholar was at Federal University of Sao Carlos, Brazil from 2001 to 2002, which was supported by both of CAPES of Brazil and of the Chinese Scholar Council. The authors thanks Mr. Carlos Casali for technique assistance.

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